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INFERRING GENET DEVELOPMENT: INTERPLAY OF MERISTEM COMMITMENT AND GENET INTEGRITY

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ABSTRACT. Canada mayflower (*Maianthemum canadense*) is a rhizomatous, perennial herb whose genets consist of multiple ramets. In a given year, ramets exist as either flowering or vegetative shoots. The production of a flowering shoot requires the commitment of the apical meristem. The identity of ramets (vegetative, flowering, or absent) directly basipetal and acropetal to a focal ramet along a linear rhizome is here termed the context of the focal ramet. A given ramet may transition from one context to another over a given year. Transitions in shoot type (a consequence of meristem commitment) occur within a developmental phase while transitions involving loss of genet integrity (a consequence of fragmentation) result in a change in phase. Each ramet begins as an acropetal ramet and transitions through several phases before becoming "isolated" (not connected to a basipetal or acropetal ramet). In this study, ages of ramets varied significantly, with flowering shoots more likely to be produced by older ramets than vegetative shoots. Isolated ramets were older on average than ramets in all other phases. The contexts and phases occupied by vegetative ramets differed significantly from those occupied by flowering ramets. Ramets producing a flowering shoot were more likely than expected to be isolated (> 50% in both years) while isolated ramets with a vegetative shoot were more likely than expected to produce a flowering shoot in the following year. Ramets with a vegetative shoot were more likely than expected to produce a vegetative shoot next year if the ramet was connected to both basipetal and acropetal ramets.

Key Words: ramet, genet, meristem, Canada mayflower, Liliaceae, *Maianthemum*

Clonal plant populations may exist as an assemblage of genets, where a genet is all the plant material derived from a single zygote (Eriksson and Jerling 1990). Each of these genets, or genetic individuals, may in turn exist as a population of potentially independent ramets (Cook 1985), where ramets are the fundamental units of plant architecture that are iterated during clonal growth (Harper 1977). How these ramets, collectively derived from a single seed, exist within the genet may vary along a continuum of organization (Harper 1985). At one end of this continuum is a genet that consists of all connected ramets and at the other end is a genet composed of all isolated ramets. In between these extremes, a genet may exist as a group of genet fragments, each composed of a variable number of connected ramets (Tuomi and Vuorisalo 1989).

The potential for "connectedness," or integration, of a species is thought to be of ecological and evolutionary significance and is the consequence of the interplay of forces promoting fragmentation and connectedness of genets. Evolutionary factors promoting fragmentation include the potential for disease spread through connections, the respiratory cost of connections, and localization of damage through disturbance. Those factors promoting connectedness include buffering of spatial variation, increased survivorship of ramets/genets through translocation of resources, and control of spatial spread to reduce intra-clonal competition (Abrahamson 1980; Cook 1985; Hutchings and Bradbury 1986; Hutchings and Mogie 1990; Pitelka and Ashmun 1985).

Canada mayflower (*Maianthemum canadense* Desf.) is a rhizomatous, perennial herb common to the understory of forests in New England. Canada mayflower is clonal with genets consisting of multiple ramets. Ramets consist of a rhizome with several nodes and an erect shoot. Each node is composed of 2–3 scale leaves, an axillary bud, and several adventitious roots (Kana 1982). Rhizome growth is sympodial with a ramet added to the genet through the activation of a lateral bud at the base of an erect shoot or an axillary bud at a node (Kana 1982).

Erect shoots are separated by an average of 12.5 cm (Ganger 1998) and their growth is essentially monopodial. A new vegetative shoot (an aerial leaf with 2–3 scale leaves and an axillary bud) is produced each year on the same axis. The growth of this axis ceases with the production of a flowering shoot (a stem, 2–3 leaves, and a terminal inflorescence). Regrowth of the erect shoot occurs with the activation of one of the previously produced subtending axillary buds (Kana 1982; Figure 1).

In the fall, vegetative shoots abscise leaving behind an overwintering bud that is preformed to become either a vegetative shoot (if an axillary bud) or a flowering shoot (if an apical bud) in the following year. Allocation of the appropriate meristem (apical or axillary) occurs at least as early as May in the year preceding emergence (Kana 1982). Whether the bud represents a vegetative or flowering shoot is here termed "bud type."

It is possible to age ramets and determine their reproductive history (whether the shoots of a given ramet have been vegetative or flowering in each year), since the vegetative and flowering shoots result from the

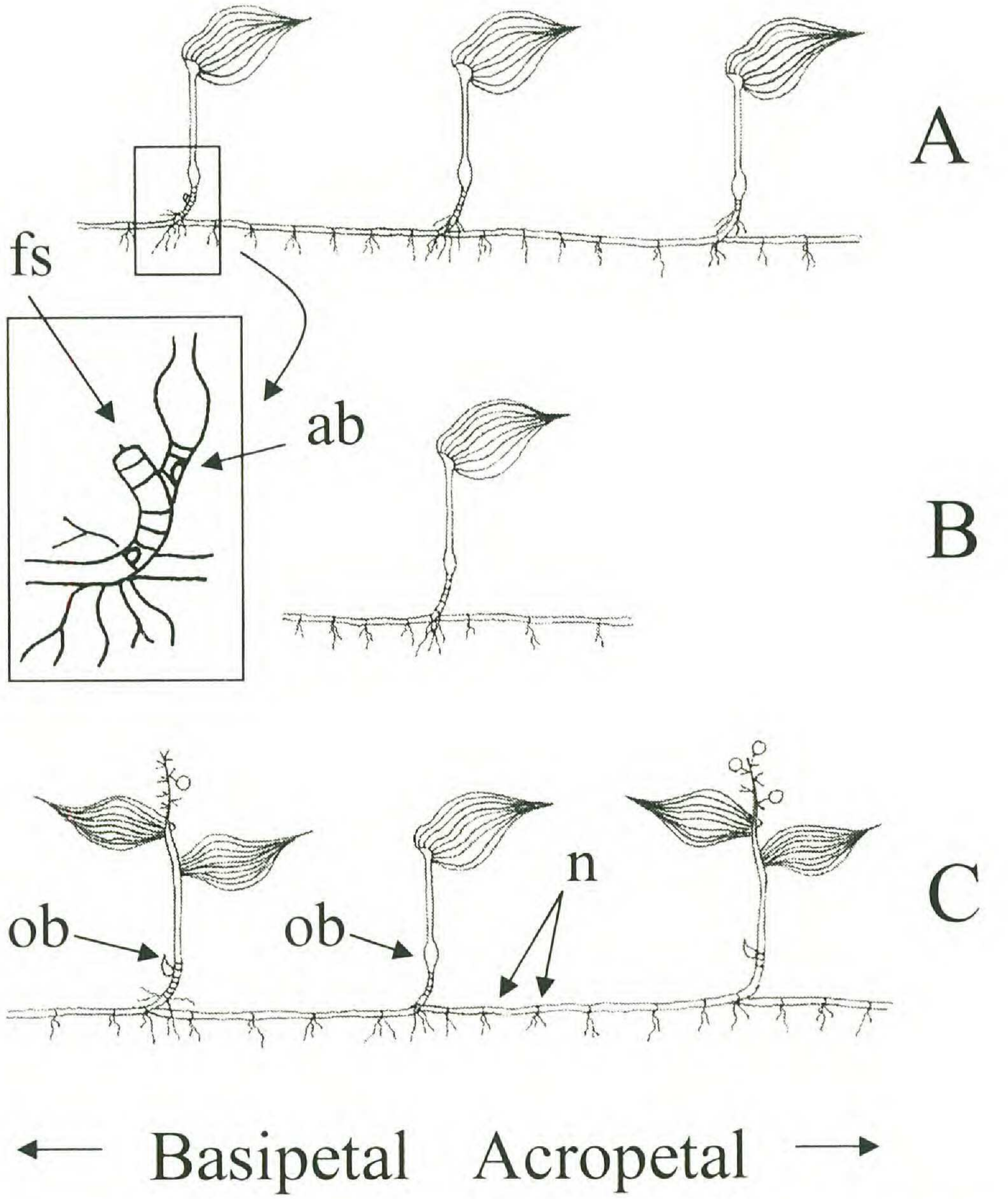

Figure 1. Three contexts of *Maianthemum canadense* are presented: A. A vegetative ramet with a vegetative ramet both basipetal and acropetal. B. A vegetative ramet with no ramet basipetal or acropetal. C. A vegetative ramet with a flowering ramet both basipetal and acropetal. n = node, fs = flowering shoot scar, ab = axillary bud, ob = overwintering bud. Note the different appearance of these buds on flowering and vegetative ramets.

commitment of different meristems and the scarring from abscission in the fall is distinctive for vegetative and flowering shoots (for a detailed explanation see Ganger 1997, Kana 1982). Hereafter, a "vegetative ramet" is defined as a ramet whose erect shoot is in the vegetative condition in the current year, and a "flowering ramet" is defined as a ramet whose erect shoot is in the flowering condition in the current year.

The habit of Canada mayflower and similar clonal plants presents an interesting situation where commitment of an apical meristem is possible and this "decision" is also being made by adjacent ramets on the same rhizome system. Adjacent ramets include the basipetal ramet, toward older tissue, and the acropetal ramet, toward younger tissue (Figure 1). Ramets are probably experiencing different physiological and microenvironmental conditions (Marshall 1990) and these differences may or may not lead to commitment of their apical meristem. If the commitment of a ramet's apical meristem is influenced by other ramets of the same genet then adjacent ramets are likely to have a greater effect than more distant ones (Cook 1985; Vuorisalo et al. 1997). The influence of adjacent ramets may vary as their identity varies (whether they currently exist as flowering shoots, vegetative shoots, or are absent). In the extreme case, a vegetative ramet connected to two vegetative ramets is potentially experiencing a different physiological condition than a vegetative ramet that is not connected to other ramets or is connected to two flowering ramets (Figure 1). The vegetative ramet in two of the three cases (Figure 1A and 1C) exists as part of a genet segment that includes three total ramets. In addition, these two focal vegetative ramets may have the same reproductive history and the same age. They do, however, differ from each other in the manner in which adjacent ramets on the same genet segment have committed meristems. Differences in states between these adjacent ramets may have an effect on how the vegetative ramets themselves commit meristems since adjacent ramets are part of the unique environmental background that ramets experience (Watson 1990). The identity (whether a vegetative shoot, flowering shoot, or not present) of these adjacent ramets (basipetal and acropetal) is here termed the "ramet context" of a focal ramet.

Fifteen distinct contexts are possible for Canada mayflower. These contexts are possible for both vegetative (15) and flowering (15) ramets, therefore, there are 30 total combinations (Figure 2). Moreover, ramets are likely to transition from one context to another over a given year. These include 1) transitions due to the commitment (or lack of commitment) of an apical meristem and 2) transitions due to fragmentation, which is the loss of connection between two ramets. These transitions may be due to mortality of the basipetal, acropetal, or both ramets or may be due to decay of the rhizome between ramets (Figure 1A). Contexts may then be grouped into six "phases:" A) a flowering or vegetative ramet basipetal and no ramet yet produced acropetally, B) no ramet basipetal (either dead or decayed rhizome) and no ramet yet produced acropetally, C) no ramet basipetal and either a vegetative or flowering ramet acropetal, D) either

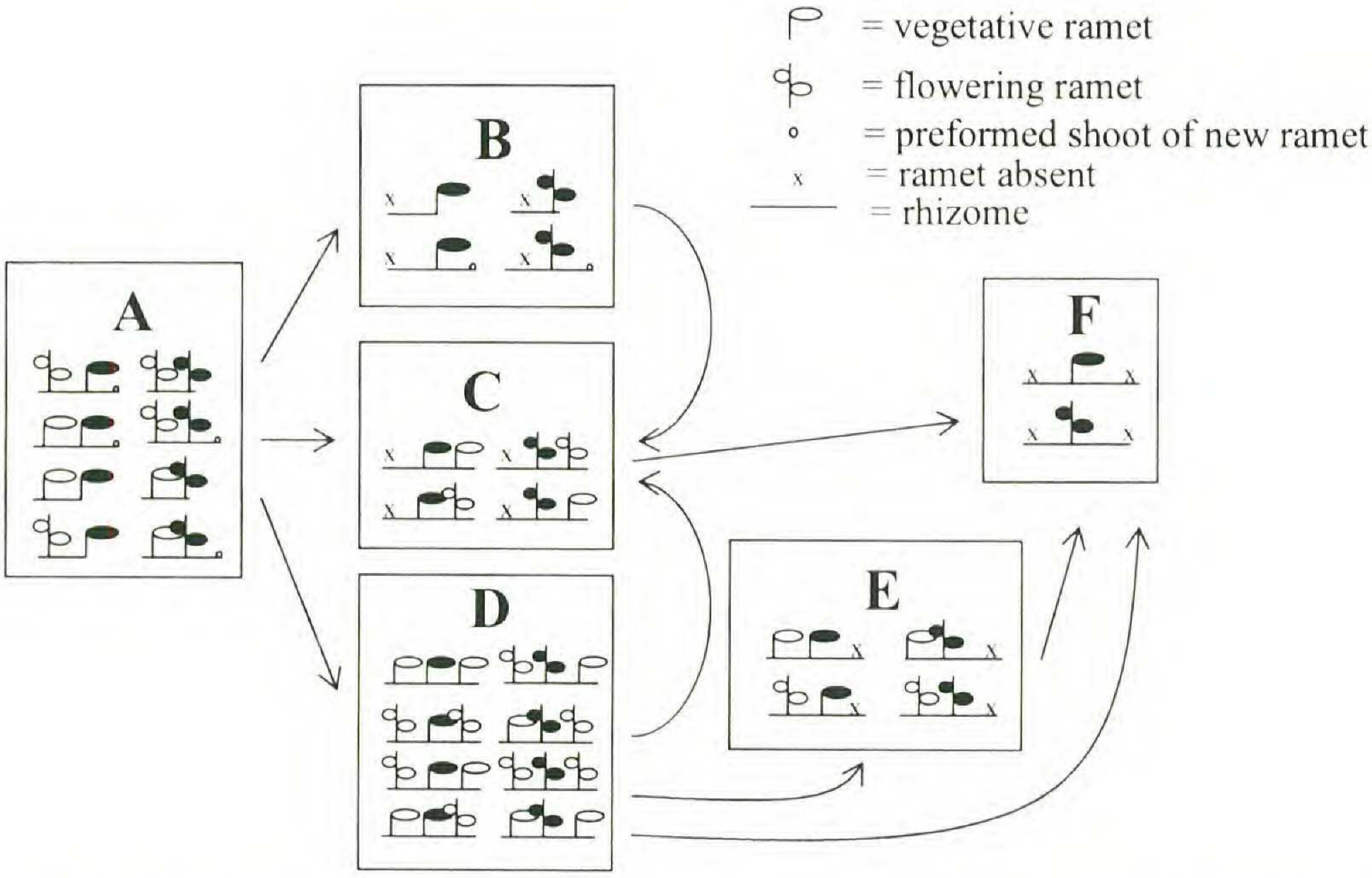

Figure 2. Six phases of *Maianthemum canadense* are presented (A–F). Each phase consists of multiple contexts. Black leaves indicate the focal ramet. Arrows indicate possible transitions from one year to the next.

a vegetative or flowering ramet both basipetal and acropetal, E) either a vegetative or flowering ramet basipetal and no ramet acropetal, and F) no ramet basipetal or acropetal (Figure 2). Transitions from one context to another within a phase are due to meristem commitments whereas changes in genet integrity necessitate transition from one phase to another.

The importance of context and phase in understanding how genets develop and how meristems are committed is not known. A two-year experiment was undertaken with Canada mayflower in order to answer the following questions: 1) What are typical ramet contexts? 2) Does ramet age vary with phase? 3) Is the distribution of vegetative and flowering ramets independent of phase? 4) Is the commitment of the apical meristem independent of phase? and 5) Is the commitment of the apical meristem related to estimated leaf surface area of vegetative ramets?

MATERIALS AND METHODS

In early spring of 1997, seven sites were identified, based on the presence of Canada mayflower, within the University of New Hampshire College Woodlands, Durham, NH (43°5.5′ north latitude, 71°25′

longitude). Sites were separated by at least 50 m. Within each site, two plots were delineated that were separated by < 1 m. Prior to emergence of shoots in one of the plots, 30 buds were identified that would become flowering shoots. In the other plot, 20 buds were identified that would become vegetative shoots. Flowering and vegetative shoots were identified in separate plots in order to increase the likelihood that vegetative ramets were physically independent of flowering ramets and meet the assumption of independence for the statistical analyses.

At the end of the fruiting season, genet segments were excavated to include the focal ramet (vegetative or flowering) and any ramets basipetal and acropetal on the same rhizome. Genet segments were labeled and taken to the laboratory. A similar procedure was followed in 1998 involving seven separate sites (consisting of two patches each) that were distinct from those in 1997.

Typical ramet contexts were divided into two subcategories: flowering ramet contexts and vegetative ramet contexts. The reason for this division was that in local populations, the frequency of flowering ramets can vary dramatically among sites (Silva et al. 1982; Worthen and Stiles 1986; Ganger, unpubl. data) and ramet contexts may differ between vegetative and flowering ramets. In this way the determination of typical ramet contexts will not be biased by the frequency of flowering ramets in a site.

For each genet segment excavated, the ramet context was determined and classified based on the identity of the ramet basipetal and acropetal on the same rhizome system: 1) no ramet basipetal or acropetal (0,0), where no ramet indicates that there is either a dead ramet or that the rhizome has decayed such that any physical connection that may have existed is no longer present; 2) vegetative ramet basipetal and no ramet acropetal (v,0); 3) no ramet basipetal and a vegetative ramet acropetal (0,v); 4) a vegetative ramet both basipetal and acropetal (v,v); 5) a flowering ramet either basipetal or acropetal (f); and 6) the presence of a newly activated lateral bud at the base of the ramet that results in a new rhizome and a new ramet acropetal, regardless of basipetal condition (b).

In order to determine whether flowering and vegetative ramets were equally distributed among contexts and phases (Figure 2), two separate three-way analyses were performed using a log-linear model (Sokal and Rohlf 1995; Wilkinson 2002). The log-linear models here are used to determine if observed frequencies of vegetative and flowering ramets in each context and phase for both years differed from expected frequencies. The expectation is that both vegetative and flowering ramets will be equally represented in each context and phase for both years.

An analysis of variance (ANOVA) was used to determine if age varied with phase. The dependent variable was ramet age. Variables included in the analysis were year, site {year}, phase, ramet type, and the two-way interactions. Year, phase, and ramet type were fixed factors, while sites were nested within year. The three-way interaction was not included due to a problem with the distribution of phases among ramets between years.

In order to determine if the commitment of the apical meristem by vegetative ramets was independent of phase, a three-way analysis was performed using a log-linear model (Sokal and Rohlf 1995; Wilkinson 2002). This analysis is used to determine if meristem commitment was independent of phase and year. This log-linear analysis included only vegetative ramets since regrowth of the shoot from a subtending axillary bud occurs after flowering. This bud is vegetative.

A regression analysis was performed to determine if estimated leaf surface area was related to the tendency for vegetative ramets to allocate the apical meristem. For vegetative ramets, the leaf surface area was estimated based on an established relationship between the leaf surface area (mm^2) and two linear measures (mm) of the leaf. The length (L) from the tip of the leaf to the base of the leaf and the width (W) of the leaf at the midpoint of the length segment together predict leaf surface area (area = $27.78*L + 55.00*W - 1198.16$; $p < 0.001$, adjusted $r^2 = 0.94$; Ganger 1998).

RESULTS

Thirty-nine of 210 flowering ramets and 9 of 140 vegetative ramets from 1997 were lost or could not be accurately aged due to decay, and were excluded from the age analysis. Forty-two of 210 flowering ramets and 6 of 140 vegetative ramets from 1998 were excluded for similar reasons.

Flowering ramets and vegetative ramets were represented in each of the six contexts in both 1997 and 1998 (Table 1) and the distribution of these ramets was not independent of context (Pearson $\chi^2_{16,\ 0.05} = 98.6$, $p < 0.001$). Deviations of the multiplicative parameter estimates from one (Wilkinson 2002) were used to assess whether the frequency of ramets in each context differed from expected. The value that is compared to one is given in parenthesis for each comparison. A value close to one indicates frequencies approaching expected while values far from one indicate values much higher or lower than expected. Vegetative ramets were more likely than expected to be connected to a vegetative ramet both basipetal and acropetal (1.52) than were

Table 1. The distribution of vegetative and flowering ramets in each of the *Maianthemum canadense* ramet contexts for both 1997 and 1998. 0 = no ramet or dead ramet, v = vegetative ramet, f = flowering ramet, and b = growing rhizome or new acropetal bud. The first symbol in the pairs represents the basipetal ramet and the second, the acropetal ramet.

	1997				1998			
	v		f		v		f	
Ramet Context	n	(%)	n	(%)	n	(%)	n	(%)
0,0	35	(26.3)	102	(53.1)	59	(43.3)	114	(62.3)
0,v	37	(27.8)	46	(24.0)	40	(29.4)	34	(18.6)
v,0	10	(7.5)	11	(5.7)	5	(3.7)	3	(1.8)
v,v	23	(17.3)	10	(5.2)	9	(6.6)	6	(3.6)
f	6	(4.6)	18	(9.4)	0	(0.0)	16	(6.6)
b	22	(17.0)	5	(2.6)	23	(16.9)	10	(8.7)

flowering ramets. Vegetative ramets were also more likely than expected to have produced an acropetal ramet (1.83). Flowering ramets were more likely than expected to be connected to other flowering ramets (2.24) and to have no ramet either basipetal or acropetal (1.44). In fact, the majority of flowering ramets in both years existed with no ramet basipetal or acropetal (51.2% in 1997, 61.7% in 1998). There were more ramets in 1998 than expected within the no ramet basipetal or acropetal context (1.33). There were more ramets in 1997 than expected within the vegetative ramet basipetal and no ramet acropetal context (1.40).

The age of ramets varied with phase ($p < 001$; Table 2; Figure 3). Ramets in phase F were significantly older than ramets in all other phases (Bonferroni adjusted $p < 0.001$; Figure 3). Ramets in phase C were significantly older than ramets in phase A (Bonferroni adjusted $p < 0.05$; Figure 3). Flowering ramets were significantly older (mean = 5.4 years, SD = 1.98, SE = 0.11) than vegetative ramets (mean = 3.9 years, SD = 1.92, SE = 0.12; $p < 0.001$; Table 2; Figure 4).

Vegetative ramets were represented in each of the six phases in both years while flowering ramets were present in all except phase A in 1998 (Table 3). The distribution of vegetative and flowering ramets was not independent of phase (Pearson $\chi^2_{16,\,0.05} = 87.6$, $p < 0.0001$). Deviations of the multiplicative parameter estimates from one indicated that more vegetative ramets than expected occurred in phases A (3.0) and B (1.3). Similarly, more flowering ramets than expected occurred in phases B (1.3), E (1.5), and F (1.8).

Twenty-five percent of vegetative ramets produced a flowering bud in 1997, while 18% produced a flowering bud in 1998. The distribution of

Table 2. Results of analysis of variance using age as the dependent variable. Y = year, P = phase, R = ramet shoot type. Adjusted $r^2 = 0.29$.

Source	df	MS	F	p-value
Year	1	14.53	1.20	NS
Site {year}	12	12.16	3.70	<0.001
Phase	5	37.09	11.30	<0.001
Ramet shoot type	1	60.96	18.57	<0.001
Y*P	5	0.67	0.20	NS
Y*R	1	0.06	0.02	NS
P*R	5	2.67	0.81	NS
Y*P*R				
Error	582	3.28		

vegetative and flowering buds was not independent of phase (Pearson $\chi^2_{16,\ 0.05} = 32.0$, $p < 0.01$). Deviations of the multiplicative parameter estimates from one indicated that more vegetative buds than expected occurred in phases A (1.7) and D (1.4). Similarly, more flowering buds than expected occurred in phases B (1.3) and F (1.5).

The estimated leaf surface area of vegetative ramets ranged between 1122 mm^2 and 4880 mm^2 in 1997, and 737 mm^2 and 3635 mm^2 in 1998. Vegetative ramets that produced a flowering bud had significantly larger leaf surface area than ramets that produced a vegetative bud ($F_{1,\ 254,\ 0.05} = 22.51$, $p < 0.001$). No vegetative ramet in either year with a leaf surface area of less than 1371 mm^2 produced a flowering bud.

DISCUSSION

Clonal plants exist as a hierarchy of organization that includes meristems, ramets, genet fragments, and genets. Here an attempt is made to place ramets, the functional units of plant construction, within the context of genet fragments to determine whether the genet fragment level of organization offers additional insights into meristem determinations made by ramets that the ramets alone would not provide.

A ramet existing as a vegetative shoot in year x may be either a vegetative shoot or a flowering shoot in year x+1. Ramets that exist as a flowering shoot in year x appear to be programmed to be a vegetative shoot in year x+1. Ramets have the potential, then, to transition between vegetative and flowering shoots. A ramet appears to flower at a maximum rate of once every two years. The rate at which mayflower ramets flower is much lower than the theoretical maximum.

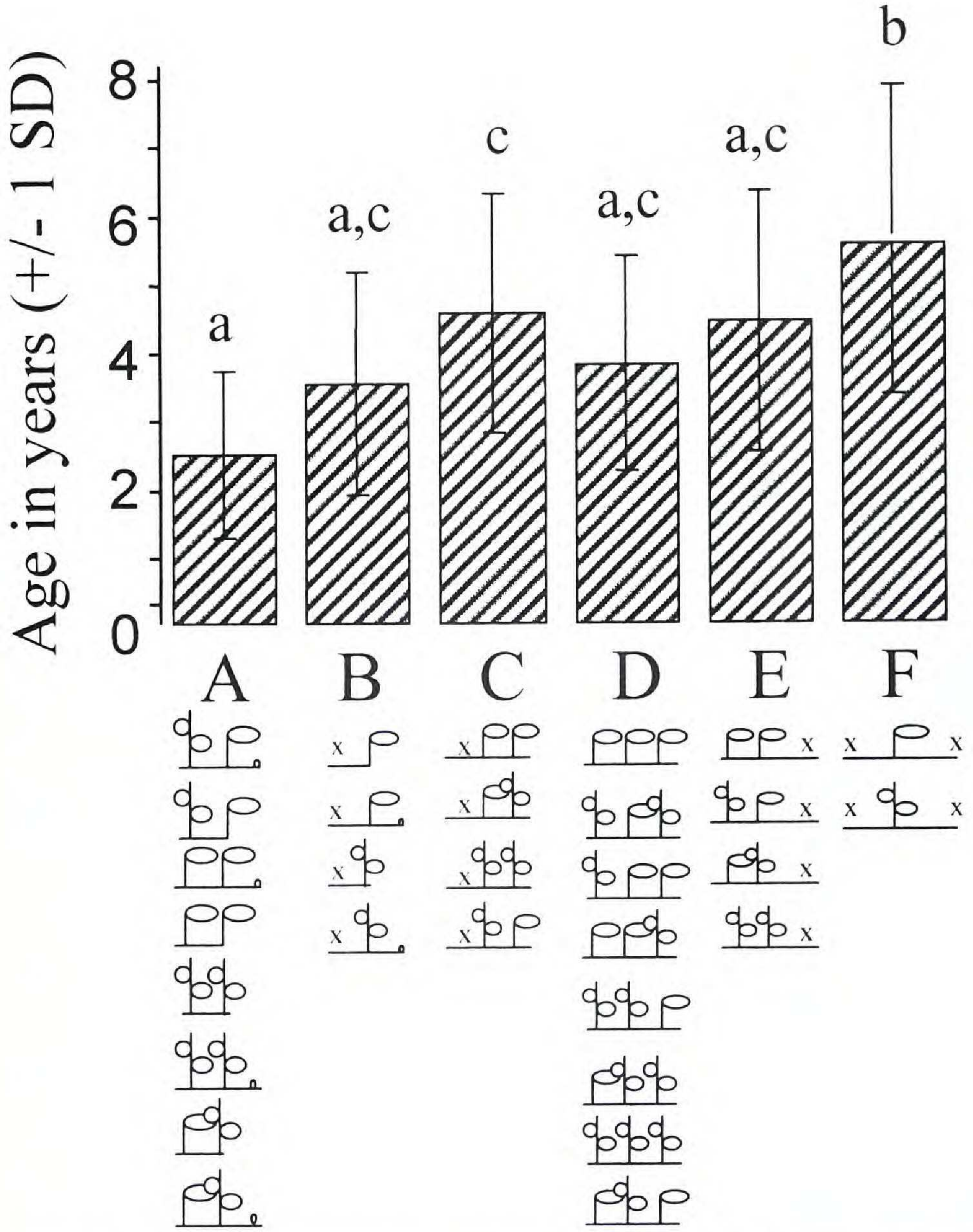

Figure 3. Ages of *Maianthemum canadense* ramets in the six phases. Small case a–c indicate means that are not significantly different. SD = standard deviation.

Despite the fact that ramets may transition between vegetative and flowering shoots, there is a significant difference in the contexts of ramets existing as vegetative and flowering shoots. It is possible that differences in their contexts represent a pre-flowering and post-flowering existence. This difference in the distribution of vegetative and flowering ramets among contexts is most evident in that vegetative ramets were more likely to be connected to one or both adjacent ramets (73.7% of ramets in populations in 1997 and 56.7% of ramets in populations in 1998; Table 1). Flowering ramets were more likely to be separated from

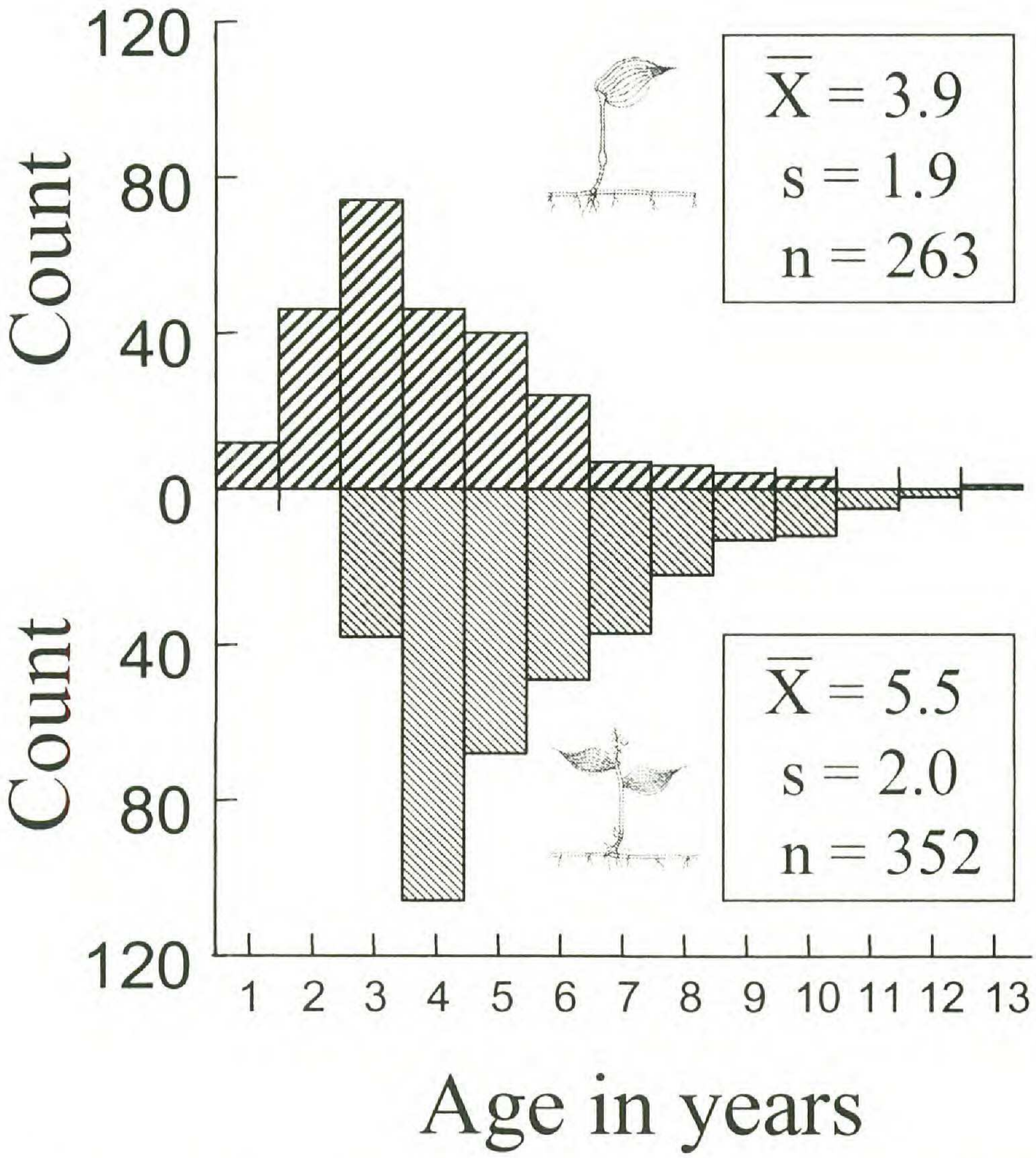

Figure 4. Distribution of the ages of *Maianthemum canadense* ramets. Vegetative ramets and flowering ramets are presented separately.

adjacent ramets, in populations of ramets in both 1997 (53.1%) and 1998 (62.3%; Table 1). The average age of flowering ramets coincided with the average age of isolated ramets in general, indicating that at least statistically, ramets are likely to flower at about the same time that they become isolated. The potential for adjacent ramets in many clonal plant species to provide photosynthates to ramets experiencing stress or periods of high resource demand, for example flowering and fruiting, is well documented (Hartnett and Bazzaz 1983; Jónsdóttir and Callaghan 1989; Turkington and Harper 1979; Yu et al. 2002). Isolated ramets would not be able to reap the benefits of integration in the year of flowering. This appears to set up an important distinction between isolated and connected flowering ramets. Do these two populations of

Table 3. The distribution of *Maianthemum canadense* ramets among phases for both 1997 and 1998. v = vegetative ramet, f = flowering ramet. Phases are illustrated in Figure 2.

	1997		1998	
Phase	v	f	v	f
A	9	1	4	0
B	13	4	19	10
C	39	56	40	42
D	27	14	9	10
E	10	16	5	8
F	35	102	59	114

flowering ramets (isolated versus connected) differ in their abilities to set and mature fruit? Or, conversely, have flowering ramets already accumulated sufficient resources independently or through prior photosynthate translocation during previous years when connections to adjacent ramets still existed?

Previous research with Canada mayflower suggests that under "typical" levels of fruiting, ramets are able to mature consistent numbers of seeds whether they are connected or experimentally isolated. Under augmented pollination, ramets were able to mature additional seeds if they were connected, but produced fewer seeds when they were experimentally isolated (Ganger 1997). Populations of flowering ramets were able to mature similar numbers of seeds whether they were flowering for the first or second time, and the relationship between the number of seeds and the average weight of these seeds was consistent between these two flowering ramet groups (Ganger 2000). The ability of a vegetative ramet to become a flowering ramet in the following year could then be thought of as an allocation response, one that is made once sufficient resources have been accumulated.

Phase also appears to be a useful construct, not just in helping to simplify the many transitions possible from context to context over a given year, but also in relating both age and the likelihood of allocating an apical meristem to changes in genet integrity. A ramet begins as a vegetative shoot, produced by a basipetal ramet. Many pathways through phases are possible from this point (Figure 2), but all pathways end ultimately in the same phase, that of an isolated ramet. Despite the existence of these multiple pathways, ramets occur with greater probability in certain phases. This pattern indicates that certain pathways are used more often as ramets mature. The average ages of ramets within phases may also be used to infer details about how the genet is developing over time. The length of time it takes for the average ramet to produce an acropetal ramet is somewhat longer than 3.5 years. This conclusion is inferred from the average ages of ramets in phase A (2.5 years) and phase B (3.5 years). A ramet's loss of connection to its genet is likely to progress over 5.5 years since ramets in phase F are 5.5 years old on average. Movement into phase F represents the loss of connection to both the basipetal and acropetal ramet. In most cases it appears that the basipetal connection is lost before the acropetal connection since only 5.7% of vegetative ramets and 6.8% of flowering ramets existed in phase E. Conversely, 32% and 30% of vegetative ramets existed in phases B and C, respectively, and 4% and 28% of flowering ramets existed in phases B and C, respectively. A ramet is unlikely to remain connected to both a basipetal and acropetal ramet (phase D) for long, since few ramets were found in this phase (13.8% of vegetative ramets and 6.8% of flowering ramets) and the average age of ramets in this phase was 3.8 years.

The phase of a vegetative ramet was also related to the probability of it committing its apical meristem to flowering in the following year. Isolated vegetative ramets were more likely to allocate apical meristems. Many plants preform organs in one year for expansion in the next (Geber et al. 1997). Whether a bud is flowering or vegetative may be related not only to current conditions but to past conditions as well (Geber et al. 1997). That ramets exist in locations with distinct edaphic and climatic conditions is generally accepted (Marshall 1990). These microenvironmental conditions may have an effect on whether a ramet's apical meristem is activated. Environmental effects on ramets may be integrated by the genet. Therefore adjacent ramets may play a role in allocation decisions of a focal ramet. Results from this study suggest two hypotheses for further testing. The first hypothesis is that as the genet begins to fragment—particularly the connection between a focal ramet and its acropetal ramet—there is a loss of apical dominance. With the loss of apical dominance comes the ability of the focal ramet to allocate its apical meristem. The second hypothesis is that ramets pass through predictable phases as they age and that the fragmentation of the genet is correlated with but not the cause of the transition from vegetative to flowering shoot. Ramets may be thought of as accumulating resources that will promote flowering. The length of time that it takes to accumulate these resources coincides with the length of time that ramets tend to remain connected to adjacent ramets.

The estimated leaf surface area of vegetative ramets was strongly correlated with the likelihood that the vegetative ramet contained a preformed flowering shoot. These results are consistent with those found by Williams (1985) for Canada mayflower and Geber et al. (1997) for mayapple (*Podophyllum peltatum*). These variables are correlated and as such it cannot be said that a larger surface area causes the commitment of an apical meristem, particularly since the bud primordia of vegetative shoots are visible under the microscope as early as May in the year prior to emergence (Kana 1982). It is entirely possible that larger leaf surface area is part of the process leading to flowering in that the greater surface area may lead to greater accumulated photosynthates.

The connections between ramets of a genet of Canada mayflower were classified as long-lived (> 2 years) by Pitelka and Ashmun (1985) using data from Silva (1978). Eriksson and Jerling (1990) classify Canada mayflower as a species with *integrated genets* as opposed to one with *genet splitters*. This classification is based in part on data from Sobey and Barkhouse (1977) that list distances between ramets on the same genet as > 40 cm. Forty cm is considered a short enough distance for translocation to still be cost effective while longer distances may result in an increased rate of disintegration (Eriksson and Jerling 1990). The length of time that inter-ramet connections must remain intact for a species to be considered an integrated genet is somewhat arbitrary. Among mayflowers, there appears to be great variation among genets in the length of time that these connections persist. Ramets as young as 2 years were found to have no ramet basipetal (phase C) and ramets as young as 1 year were found to have no ramet basipetal or acropetal (phase F). Conversely, ramets as old as 8 years were found to still have a ramet both basipetal and acropetal (phase D) and ramets as old as 9 years were found to still have a ramet basipetal (phase B). This variability may be as important as the average length of time that these connections persist in Canada mayflower since it suggests either phenotypic plasticity in the persistence of connections or the potential for genetic variation with respect to the persistence of connections. Effectively then, the responses ascribed to genets by Eriksson and Jerling (1990) may be responses of ramets. The overall effect of these ramet responses would be evident at the level of the genet. To the degree that genets appeared to act differently, there would be uniformity of action by ramets within a genet. If there is a great deal of phenotypic plasticity in disintegration behavior, then how genets are categorized becomes less important. If there is uniformity of behavior by ramets (i.e., low levels of phenotypic plasticity) within a genet, the genets may effectively be categorized.

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